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A revised generic classification of vittarioid ferns (Pteridaceae) based on molecular, micromorphological, and geographic data

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Abstract Vittarioid ferns compose a well-supported clade of 100–130 species of highly simplified epiphytes in the family Pteridaceae. Generic circumscriptions within the vittarioid clade were among the first in ferns to be evaluated and revised based on molecular phylogenetic data. Initial analyses of *rbcL* sequences revealed strong geographic structure and demonstrated that the two largest vittarioid genera, as then defined, each had phylogenetically distinct American and Old World components. The results of subsequent studies that included as many as 36 individuals of 33 species, but still relied on a single gene, were generally consistent with the early findings. Here, we build upon the previous datasets, incorporating many more samples (138 individuals representing 72 species) and additional plastid markers (*atpA*, *chlN*, *rbcL*, *rpoA*). Analysis of our larger dataset serves to better characterize known lineages, reveals new lineages, and ultimately uncovers an underlying geographic signal that is even stronger than was previously appreciated. In our revised generic classification, we recognize a total of eleven vittarioid genera. Each genus, including the new genus *Antrophyopsis* (Benedict) Schuettp., stat. nov., is readily diagnosable based on morphology, with micromorphological characters related to soral paraphyses and spores complementing more obvious features such as venation and the distribution of sporangia. A key to the currently recognized vittarioid genera, brief generic descriptions, and five new species combinations are provided.

Keywords Africa; epiphytes; paraphyses; phylogeny; pteridophytes; spores; taxonomic revision

Supplementary Material Electronic Supplement (Fig. S1) and DNA sequence alignments are available in the Supplementary Data section of the online version of this article at http://ingentaconnect.com/content/iapt/tax

■ INTRODUCTION

In ferns, as in most branches of the tree of life, phylogenetic analyses of molecular data have greatly improved our ability to identify natural groupings that are subsequently reflected in classifications grounded in the principle of monophyly (Smith & al., 2006; Rothfels & al., 2012; Christenhusz & Chase, 2014). In some cases, the results of such analyses are consistent with earlier notions of relationships inferred from morphological features (Schneider & al., 2009). However, in many other instances, lineages are revealed that are morphologically confounding and we struggle to identify synapomorphies (Sundue & Rothfels, 2014). The pursuit of such defining characteristics is especially problematic when working within a group possessing very limited morphological disparity.

The well-defined vittarioid fern clade consists of 100–130 (Lindsay, 2003) highly simplified and predominantly epiphytic species (Fig. 1). These plants, characterized by the presence of silica bodies (Sundue, 2009) but a lack of sclerenchyma (Bower 1928; Ruhfel & al., 2008), were long regarded as composing a distinct family—Vittariaceae (Ching, 1940; Tryon & Tryon, 1982; Kramer, 1990). However, phylogenetic analyses have demonstrated that these ferns nest well within the Pteridaceae (Crane & al., 1995; Hasebe & al., 1995; Prado & al., 2007; Schuettpelz & al., 2007), as sister to the genus *Adiantum* L. (Lu & al., 2012; Rothfels & Schuettpelz, 2014; Pryer & al., 2016).

The vittarioids have been variously partitioned through time (Benedict, 1911; Williams, 1927; Copeland, 1947). In the years leading up to the first molecular phylogenetic analyses of these ferns, six genera were commonly recognized based primarily on leaf division, venation, and the distribution of

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Fig. 1. Vittarioid fern habits and key morphological features. **A,** Epiphytic habit of *Haplopteris elongata* (Sw.) E.H.Crane (leaves ca. 1 cm wide); **B,** Epiphytic habit, and forked leaves, of *Hecistopteris pumila* (Spreng.) J.Sm. (leaves ca. 3 cm long); **C,** Epiphytic habit of *Antrophyum annamense* Tardieu & C.Chr. (leaves ca. 5 cm wide); **D,** Epiphytic habit of *Haplopteris graminea* (Poir.) comb. ined. (= *Monogramma graminea* (Poir.) Schkuhr, leaves ca. 5 cm long): **E,** Pinnately compound leaves and round sori of *Rheopteris cheesmaniae* Alston (leaves ca. 3 cm wide); **F,** Biseriate areolate venation of *Haplopteris elongata* (leaf ca. 1 cm wide); **G,** Pluriseriate areolate venation of *Antrophyum sessilifolium* (Cav.) Spreng. (leaf about 3 cm wide); **H,** Sori of *Radiovittaria remota* (Fée) E.H.Crane, restricted to submarginal commissures (leaf ca. 1 cm wide); **I,** Sori of *Antrophyum castaneum* H.Ito, along reticulate veins (leaf ca. 3 cm wide); **J,** Sori of *Scoliosorus ensiformis* (Hook.) T.Moore, along reticulate veins (leaf ca. 2 cm wide); **K,** Sori of *Vaginularia acrocarpa* Holttum, appearing as one continuous line on each leaf (leaves ca. 1 mm wide); **L,** Soral paraphyses of *Antrophyum callifolium* Blume, with slender apical cells (scale bar 100 µm); **M,** Soral paraphyses of *Antrophyum subfalcatum* Brack., with spherical apical cells (scale bar 100 µm); **N,** Soral paraphyses of *Haplopteris elongata*, with obconic apical cells (scale bar 100 µm). — Image credits: Cheng-Wei Chen (C, G, I, K, L, M, N); Fay-Wei Li (B); Germinal Rouhan (D); Eric Schuettpelz (A, F); Michael Sundue, http://www.fernsoftheworld.com (H, J); and Wayne Takeuchi (E).

sporangia (Tryon & Tryon, 1982; Kramer, 1990). The monotypic *Rheopteris* Alston was considered to be unique (among vittarioids) based on its pinnately divided leaves and round sori (Fig. 1E). The small genus *Hecistopteris* J.Sm. was also easily segregated based on its minute, forked or lobed leaves (Fig. 1B). The remaining genera were characterized by the presence of simple leaves. Among them, the monotypic *Anetium* Splitg. was readily separated from other vittarioids by having sporangia on its abaxial leaf surfaces that are not restricted to the veins. *Vittaria* Sm., with 50–80 species recognized at the time (Kramer, 1990), was defined as having sporangia confined to submarginal commissures (Fig. 1H). *Antrophyum* Kaulf. was applied to those species (about 50) with pluriseriate areolate venation (Fig. 1G) and sporangia following the veins (not confined to submarginal commissures; Fig. 1I). Finally, *Monogramma* Comm. ex Schkuhr consisted of a handful of diminutive species with sporangia borne along the singular leaf vein, or the lateral vein(s), if present (Fig. 1K).

Generic circumscriptions within vittarioids were among the first in ferns to be evaluated and revised based on molecular phylogenetic data. Although initial analyses of *rbcL* sequences (Crane & al., 1995) included only species of four of the six genera widely recognized at the time (*Rheopteris* and *Monogramma* were not sampled), they already revealed a significant lack of monophyly at the generic level. Specifically, *Vittaria* was demonstrated to include four distinct elements and *Antrophyum* three. A new phylogenetically based, and morphologically defensible, classification was thus proposed that divided *Vittaria* and *Antrophyum* (sensu Tryon & Tryon, 1982; Kramer, 1990) into four genera (*Ananthacorus* Underw. & Maxon, *Haplopteris* C.Presl, *Radiovittaria* (Benedict) E.H.Crane, *Vittaria*) and three genera (*Antrophyum*, *Polytaenium* Desv., *Scoliosorus* T.Moore), respectively (Crane, 1997). Names existed at the generic level for each of these segregates, with one exception for which a subgeneric name was elevated (*Radiovittaria*).

Crane's (1997) classification relied heavily on micromorphological characters, focusing specifically on spore type and the shape of the apical cells of the soral paraphyses (Fig. 1L–N), but also considered gross morphology and geography. Of the species with sporangia confined to submarginal commissures (formerly placed in *Vittaria*), *Ananthacorus* was readily segregated based on its pluriseriate areolate venation (all other elements had biseriate areolate venation), *Vittaria* was restricted to taxa with soral paraphyses having slender apical cells, and species with obconic apical cells were further divided based on their phyllotaxy (distichous in *Haplopteris* and polystichous in *Radiovittaria*). Of the species with pluriseriate areolate venation and sporangia following the veins (not confined to submarginal commissures; formerly placed in *Antrophyum*), those lacking soral paraphyses were placed in *Polytaenium* and those having paraphyses were placed in *Antrophyum* or *Scoliosorus* (depending on whether their spores were trilete or monolete, respectively).

Subsequent phylogenetic studies (Schuettpelz & al., 2007; Ruhfel & al., 2008) included the previously unsampled genera *Rheopteris* and *Monogramma*. The monotypic *Rheopteris* and some species of *Monogramma* (as then defined) were together found to be sister to the remaining vittarioids; other species of *Monogramma* were resolved elsewhere within the vittarioid phylogeny. Ruhfel & al. (2008) advocated for the application of the existing name *Vaginularia* Fée to those species formerly treated in *Monogramma* that were most closely related to *Rheopteris*. Lindsay & Chen (2014) placed another species formerly treated in *Monogramma* in *Haplopteris*, noting that the type species of *Monogramma* had other affinities. Recent analyses focused attention on relationships within the two largest vittarioid genera—*Haplopteris* and *Antrophyum* (Chen & al., 2013a, b, 2015). However, a well-sampled study of the overall vittarioid phylogeny, based on multiple molecular markers, has yet to be published.

Here, we build upon the earlier analyses of vittarioid fern relationships by incorporating many more samples and additional plastid markers. Analysis of our larger dataset serves to better characterize known lineages, reveals new lineages, and ultimately uncovers an underlying geographic signal that is even stronger than was previously recognized.

■ MATERIALS AND METHODS

The ingroup sampling for this study comprised 138 individuals of 72 vittarioid species (Appendix 1). An effort was made to include as many species as possible, but also to sample from across the ranges of the more widespread species. In general, no more than one individual of a given species was sampled from a particular country. However, if representatives were only obtainable from a single country, two individuals were included from that country (as available). In addition to the 138 vittarioid samples, 7 individuals representing 7 species from across *Adiantum* (Appendix 1) were included to root the vittarioid phylogeny, based on earlier studies that found a sister relationship between *Adiantum* and the vittarioids (Schuettpelz & al., 2007; Lu & al., 2012; Rothfels & Schuettpelz, 2014; Pryer & al., 2016).

Genomic DNA was typically extracted from silica-dried samples (most individuals) or herbarium fragments using a modified CTAB protocol (Doyle & Doyle, 1987), as described in detail in Beck & al. (2011). Four plastid gene regions (*atpA*, *chlN*, *rbcL*, *rpoA*) were amplified independently using the polymerase chain reaction (PCR). Nuclear gene sequencing within ferns is challenging (Schuettpelz & al., 2008) and nuclear markers were not included here. However, with the greater availability of transcriptome data and next-generation sequencing approaches, the landscape is changing (Rothfels & al., 2015).

For *atpA*, either a large region (including the entire *atpA* gene, plus portions of the *atpF* and *trnR* genes and the associated spacers) or a small region (including only a portion of the *atpA* gene) was targeted, depending mostly on the quality of each genomic DNA extraction. For the larger region, the primers (Table 1) and amplification protocol of Schuettpelz & al. (2006) were utilized, whereas for the smaller region, the primers (Table 1) and amplification protocol of Cochran &

Table 1. Amplification and sequencing primers used in this study of vittarioid ferns.

Region	Primer	Utility (direction)	Reference or sequence (if new)
atpA (large)	ESATPF412F	Amplification/sequencing (forward)	Schuettpelz & al., 2006
atpA (large)	ESATPA535F	Sequencing (forward)	Schuettpelz & al., 2006
atpA (large)	ESATPA557R	Sequencing (reverse)	Schuettpelz & al., 2006
atpA (large)	ESATPA856F	Sequencing (forward)	Schuettpelz & al., 2006
atpA (large)	ESATPA877R	Sequencing (reverse)	Schuettpelz & al., 2006
atpA (large)	ESTRNR46F	Amplification/sequencing (reverse)	Schuettpelz & al., 2006
atpA (small)	atpA-F1	Amplification/sequencing (forward)	Cochran & al., 2014
atpA (small)	atpA-R1	Amplification/sequencing (reverse)	Cochran & al., 2014
chlN	chlN-F2	Amplification/sequencing (forward)	CGWTAYGCRAYGGCVGAATYGSAAG
chlN	chlN-R2	Amplification/sequencing (reverse)	CAWATTTTTTCGATCCARGCRCGTG
rbcL	ESRBCL1F	Amplification/sequencing (forward)	Schuettpelz & Pryer, 2007
rbcL	ESRBCL628F	Sequencing (forward)	Schuettpelz & Pryer, 2007
rbcL	ESRBCL654R	Sequencing (reverse)	Schuettpelz & Pryer, 2007
rbcL	ESRBCL1361R	Amplification/sequencing (reverse)	Schuettpelz & Pryer, 2007
rpoA	rpoA-F1	Amplification/sequencing (forward)	TRCAYGAGTATTCYACAATAACGGG
rpoA	rpoA-R1	Amplification/sequencing (reverse)	AATTAAARGCTCTRGCRGGTRATTC

al. (2014) were applied. For *chlN* (a plastid gene coding for photochlorophyllide reductase subunit N), primers were newly developed (Table 1), but the amplification protocol of Cochran & al. (2014) was followed. For *rbcL*, a large segment of the gene was generally amplified (following Schuettpelz & Pryer, 2007); however, in some cases it was necessary to amplify this segment in two parts due to the quality of the genomic DNA extraction. For *rpoA* (a plastid gene coding for the RNA polymerase alpha subunit), primers were again newly developed (Table 1) and the protocol of Cochran & al. (2014) was followed, except that the annealing temperature was reduced to 45°C. Visualization and cleanup of PCR products, as well as sequencing, followed previously published protocols (Schuettpelz & al., 2006; Schuettpelz & Pryer, 2007; Cochran & al., 2014). For some individuals, sequences were already published and a total of 110 sequences were thus simply downloaded from GenBank. Because of failed amplification or sequencing reactions, 55 sequences could not be obtained, but a total of 415 sequences were newly acquired for this study and uploaded to GenBank (Appendix 1).

For each plastid gene region, the relevant sequences were assembled in AliView v.1.17 (Larsson, 2014) and initially aligned therein with MUSCLE v.3.8 (Edgar, 2004). The resulting alignments were then visually inspected, and manually edited with the guidance of corresponding amino acid translations. Because the *atpA* sequences obtained were of two distinct lengths (resulting in copious amounts of missing data in the alignment for some taxa) and also because the longer sequences incorporated non-coding flanking regions (where alignment was frequently ambiguous), the characters outside of the shorter targeted region were excluded. Details relevant to the datasets are provided in Table 2.

The four single-gene alignments were independently subjected to phylogenetic analysis in MrBayes v.3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) using the GTR+G model of sequence evolution and a temperature of 0.05. Analyses incorporated four independent runs, each with four chains, proceeded for 10 million generations, and sampled trees every 8000 generations. After completion, output files were examined for reasonable chain swap rates. To

Table 2. Details concerning the alignments used in this study of vittarioid ferns.

Dataset	Individuals	Total characters	Included characters	Variable characters	Missing data (%)*
atpA	136	1861	629	248	0.8
chlN	121	624	624	338	2.4
rbcL	142	1309	1309	483	4.3
rpoA	126	619	619	394	4.4
Combined	145	4413	3181	1463	10.9

*Calculation based on included characters.

verify that the runs had converged, the standard deviation of split frequencies was evaluated; additionally, parameter estimates were plotted and ESS values examined in Tracer v.1.6 (Rambaut & al., 2014). Based on these diagnostics, the first 250 trees (corresponding to the first 2 million generations) were very conservatively excluded before obtaining a majority-rule consensus phylogeny—with clade posterior probabilities—for each plastid gene region.

The four single-gene trees were rooted at the split between *Adiantum* and vittarioids and inspected visually for well-supported (posterior probability, PP ≥ 0.95) topological differences. Only three significant topological differences were encountered among the four gene trees, all involving shallow branches. While *atpA* supported the monophyly of the two included samples of *Haplopteris humblotii* (Hieron.) S.Linds. & C.W.Chen (9345, 9346), *rbcL* found support for their paraphyly relative to *H. guineensis* (Desv.) E.H.Crane and *H. schliebenii* (Reimers) Schuettp. Likewise, while *chlN* supported the monophyly of the two included samples of *Vittaria isoetifolia* Bory (9342, 10161), *rpoA* found support for their paraphyly relative to a sample of *V. lineata* (L.) Sm. (8927). Finally, while *chlN* supported the two included samples of *Haplopteris mediosora* (Hayata) X.C.Zhang (9694, 9695) as sister to a clade comprising *H. doniana* (Mett. ex Hieron.) E.H.Crane, *H. fudzinoi* (Makino) E.H.Crane, *H. linearifolia* (Ching) X.C.Zhang, *H. plurisulcata* (Ching) X.C.Zhang, and *H. taeniophylla* (Copel.) E.H.Crane, *rbcL* supported them as sister to *H. malayensis* (Holttum) E.H.Crane. Because the aforementioned conflicts were all inconsequential to the primary objectives of this study, the *atpA*, *chlN*, *rbcL*, and *rpoA* datasets were combined for further analysis.

The combined dataset was phylogenetically analyzed using a maximum likelihood approach, as implemented in RAxML v.8.0.3 (Stamatakis, 2014). This analysis employed the GTRGAMMA model of sequence evolution, with parameters independently estimated for each gene, and involved 1000 rapid bootstrap inferences followed by a thorough maximum likelihood search. The combined dataset was also analyzed using the Bayesian approach described above for the single-gene alignments, but with model parameters estimated separately for each gene and each run proceeding for 40 million generations. Here, trees were sampled every 32,000 generations and convergence was assessed as above; the first 8 million generations were excluded prior to calculating the majority-rule consensus phylogeny with clade posterior probabilities.

For each vittarioid species in our dataset, we assessed leaf venation pattern, the apical cell shape of soral paraphyses, spore type, geographic distribution, and, as applicable, other morphological features by examining herbarium specimens and the relevant literature.

■ RESULTS

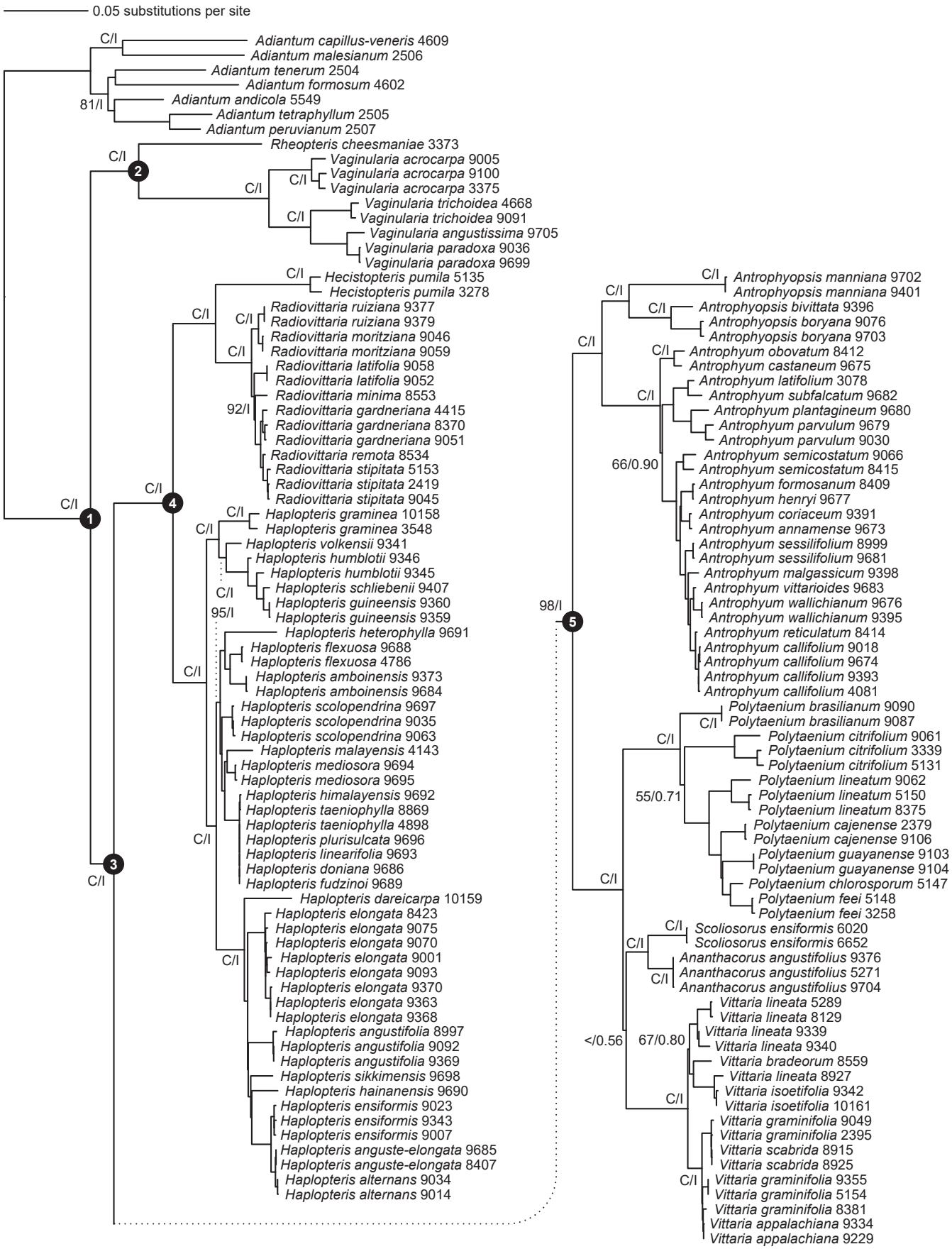
The monophyly of the vittarioids—relative to *Adiantum*—is strongly supported, with a maximum likelihood bootstrap percentage (BS) of 100 and a Bayesian posterior probability (PP) of 1.00 (node 1, Fig. 2). Within vittarioids, the first divergence is highly asymmetrical with regard to species number. The smaller clade (BS = 100; PP = 1.00; node 2, Figs. 2, 3) is characterized by free venation (pinnately compound or indistinct pinnate) and trilete spores. It consists exclusively of species from Asia and the Pacific Ocean and unites the only vittarioid genus with compound leaves (*Rheopteris*) with some of the most morphologically simplified species (treated here in *Vaginularia*). The larger vittarioid clade (BS = 100; PP = 1.00; node 3, Figs. 2, 3) consists primarily of simple-leaved species with reticulate venation but is otherwise morphologically variable. Within this larger clade, a rather symmetrical divergence separates two subclades of approximately equal size. One subclade (BS = 100; PP = 1.00; node 4, Figs. 2, 3) is characterized by paraphyses with obconic apical cells and consists almost entirely of species with biseriate areolate leaf venation. The other subclade (BS = 98; PP = 1.00; node 5, Figs. 2, 3) does not have an obvious unifying morphological feature, but includes all of the species with pluriseriate areolate leaf venation (along with six sampled species possessing biseriate areolate venation and one with parallel free veins). Within the two aforementioned subclades, a consistent biogeographic pattern emerges, with each containing a well-supported American lineage sister to a well-supported Old World lineage. In each of the two Old World lineages, there is, in turn, an African/Indian Ocean group sister to a largely Asian/Pacific Ocean group (the latter with one or a few derived African/Indian Ocean representatives).

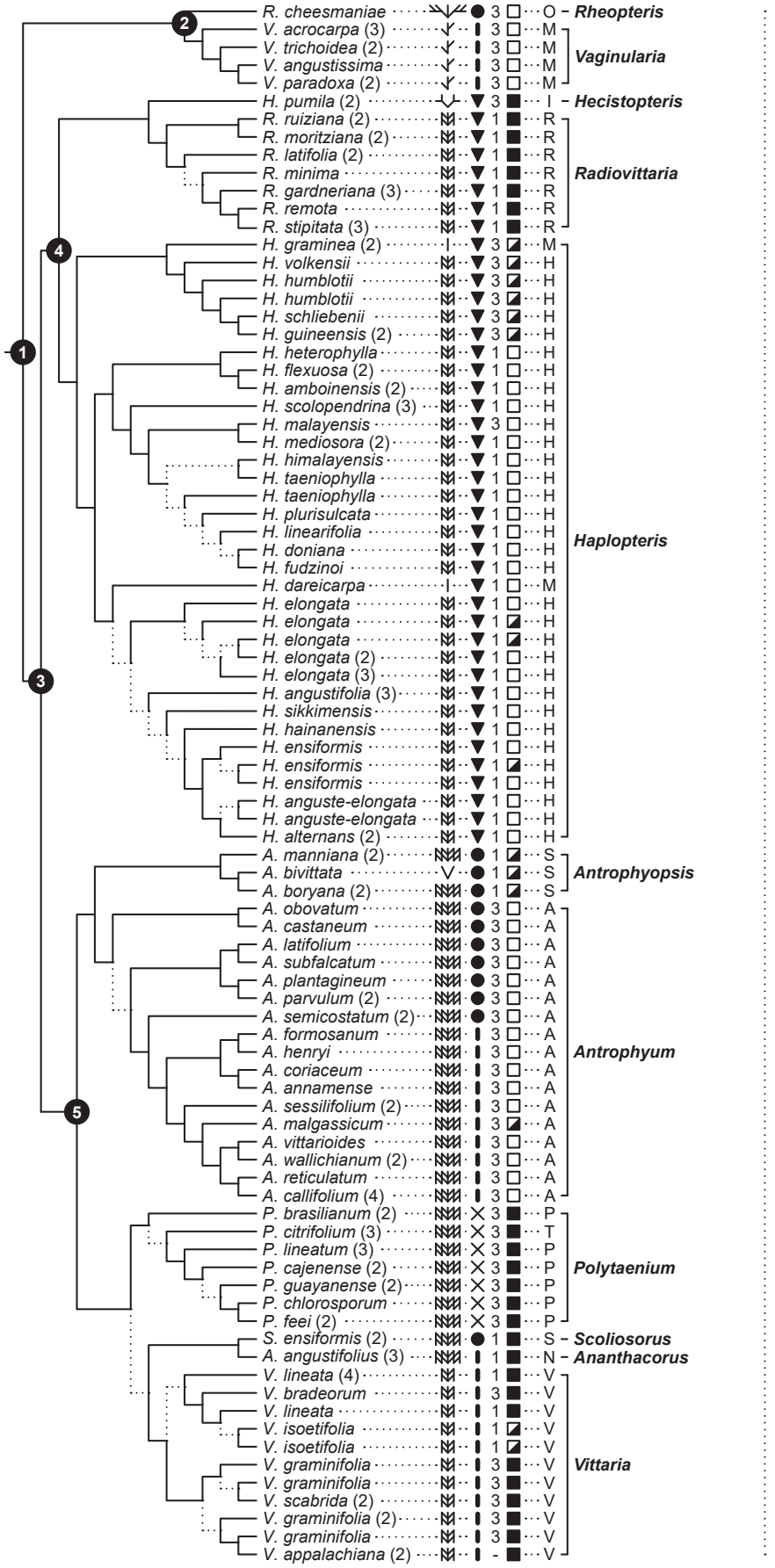
Overall, relationships within the vittarioids are reasonably well supported. Of 136 resolved nodes, 106 received good support (i.e., BS ≥ 70 *and* PP ≥ 0.95; Electr. Suppl.: Fig. S1). Nearly all (29 of 30) poorly supported nodes involve relationships among species within genera. In most (38 of 42) cases where more than one sample of a species was available for sequencing, species were resolved as monophyletic (36 of 42 received good support; Electr. Suppl.: Fig. S1).

■ DISCUSSION

Phylogeny. — The earliest molecular phylogenetic study of vittarioid ferns (Crane & al., 1995) found the two largest genera, as commonly circumscribed at the time (*Antrophyum*, *Vittaria*), to be polyphyletic. This motivated a revised classification for the group (Crane, 1997) that was able to accommodate the goal of only recognizing monophyletic genera simply through the

Fig. 2. Vittarioid fern phylogeny resulting from maximum likelihood analysis of a four-gene (*atpA*, *chlN*, *rbcL*, *rpoA*) plastid dataset incorporating 138 ingroup and 7 outgroup individuals. Maximum likelihood bootstrap percentages (BS) and Bayesian posterior probabilities (PP) are provided at select nodes (BS / PP; C = 100; I = 1.00; < = BS < 50 or PP < 0.50); support values for all nodes are provided in Fig. S1 (Electr. Suppl.). White numbers in black circles at nodes correspond to major clades / subclades discussed in the text. Species names in tree follow the generic classification proposed in this study; for previous generic assignments, see Fig. 3. Numbers following species names are Fern Lab Database (http://fernlab.biology.duke.edu) voucher numbers (Appendix 1). ▶


0.05 substitutions per site
C/I
Adiantum capillus-veneris 4609
Adiantum malesianum 2506
Adiantum tenerum 2504
Adiantum formosum 4602
81/I
Adiantum andicola 5549
Adiantum tetraphyllum 2505
Adiantum peruvianum 2507
Rheopteris cheesmaniae 3373
2
Vaginularia acrocarpa 9005
Vaginularia acrocarpa 9100
Vaginularia acrocarpa 3375
Vaginularia trichoidea 4668
Vaginularia trichoidea 9091
Vaginularia angustissima 9705
Vaginularia paradoxa 9036
Vaginularia paradoxa 9699
Hecistopteris pumila 5135
Hecistopteris pumila 3278
Radiovittaria ruiziana 9377
Radiovittaria ruiziana 9379
Radiovittaria moritziana 9046
Radiovittaria moritziana 9059
Radiovittaria latifolia 9058
Radiovittaria latifolia 9052
Radiovittaria minima 8553
92/I
Radiovittaria gardneriana 4415
Radiovittaria gardneriana 8370
Radiovittaria gardneriana 9051
Radiovittaria remota 8534
Radiovittaria stipitata 5153
Radiovittaria stipitata 2419
Radiovittaria stipitata 9045
1
4
Haplopteris graminea 10158
Haplopteris graminea 3548
Haplopteris volkensii 9341
Haplopteris humblotii 9346
Haplopteris humblotii 9345
Haplopteris schliebenii 9407
Haplopteris guineensis 9360
95/I
Haplopteris guineensis 9359
Haplopteris heterophylla 9691
Haplopteris flexuosa 9688
Haplopteris flexuosa 4786
Haplopteris amboinensis 9373
Haplopteris amboinensis 9684
Haplopteris scolopendrina 9697
Haplopteris scolopendrina 9035
Haplopteris scolopendrina 9063
Haplopteris malayensis 4143
Haplopteris mediosora 9694
Haplopteris mediosora 9695
Haplopteris himalayensis 9692
Haplopteris taeniophylla 8869
Haplopteris taeniophylla 4898
Haplopteris plurisulcata 9696
Haplopteris linearifolia 9693
Haplopteris doniana 9686
Haplopteris fudzinoi 9689
3
Haplopteris dareicarpa 10159
Haplopteris elongata 8423
Haplopteris elongata 9075
Haplopteris elongata 9070
Haplopteris elongata 9001
Haplopteris elongata 9093
Haplopteris elongata 9370
Haplopteris elongata 9363
Haplopteris elongata 9368
Haplopteris angustifolia 8997
Haplopteris angustifolia 9092
Haplopteris angustifolia 9369
Haplopteris sikkimensis 9698
Haplopteris hainanensis 9690
Haplopteris ensiformis 9023
Haplopteris ensiformis 9343
Haplopteris ensiformis 9007
Haplopteris anguste-elongata 9685
Haplopteris anguste-elongata 8407
Haplopteris alternans 9034
Haplopteris alternans 9014
98/I
5
Antrophyopsis manniana 9702
Antrophyopsis manniana 9401
Antrophyopsis bivittata 9396
Antrophyopsis boryana 9076
Antrophyopsis boryana 9703
Antrophyum obovatum 8412
Antrophyum castaneum 9675
Antrophyum latifolium 3078
Antrophyum subfalcatum 9682
Antrophyum plantagineum 9680
Antrophyum parvulum 9679
Antrophyum parvulum 9030
66/0.90
Antrophyum semicostatum 9066
Antrophyum semicostatum 8415
Antrophyum formosanum 8409
Antrophyum henryi 9677
Antrophyum coriaceum 9391
Antrophyum annamense 9673
Antrophyum sessilifolium 8999
Antrophyum sessilifolium 9681
Antrophyum malgassicum 9398
Antrophyum vittarioides 9683
Antrophyum wallichianum 9676
Antrophyum wallichianum 9395
Antrophyum reticulatum 8414
Antrophyum callifolium 9018
Antrophyum callifolium 9674
Antrophyum callifolium 9393
Antrophyum callifolium 4081
Polytaenium brasilianum 9090
Polytaenium brasilianum 9087
Polytaenium citrifolium 9061
Polytaenium citrifolium 3339
Polytaenium citrifolium 5131
Polytaenium lineatum 9062
55/0.71
Polytaenium lineatum 5150
Polytaenium lineatum 8375
Polytaenium cajenense 2379
Polytaenium cajenense 9106
Polytaenium guayanense 9103
Polytaenium guayanense 9104
Polytaenium chlorosporum 5147
Polytaenium feei 5148
Polytaenium feei 3258
Scoliosorus ensiformis 6020
Scoliosorus ensiformis 6652
Ananthacorus angustifolius 9376
Ananthacorus angustifolius 5271
Ananthacorus angustifolius 9704
Vittaria lineata 5289
Vittaria lineata 8129
</0.56
67/0.80
Vittaria lineata 9339
Vittaria lineata 9340
Vittaria bradeorum 8559
Vittaria lineata 8927
Vittaria isoetifolia 9342
Vittaria isoetifolia 10161
Vittaria graminifolia 9049
Vittaria graminifolia 2395
Vittaria scabrida 8915
Vittaria scabrida 8925
Vittaria graminifolia 9355
Vittaria graminifolia 5154
Vittaria graminifolia 8381
Vittaria appalachiana 9334
Vittaria appalachiana 9229


R. cheesmaniae 3 O Rheopteris
V. acrocarpa (3) 3 M
V. trichoidea (2) 3 M
V. angustissima 3 M
V. paradoxa (2) 3 M Vaginularia
H. pumila (2) 3 I Hecistopteris
R. ruiziana (2) 1 R
R. moritziana (2) 1 R
R. latifolia (2) 1 R
R. minima 1 R
R. gardneriana (3) 1 R
R. remota 1 R
R. stipitata (3) 1 R Radiovittaria
H. graminea (2) 3 M
H. volkensii 3 H
H. humblotii 3 H
H. humblotii 3 H
H. schliebenii 3 H
H. guineensis (2) 3 H
H. heterophylla 1 H
H. flexuosa (2) 1 H
H. amboinensis (2) 1 H
H. scolopendrina (3) 1 H
H. malayensis 3 H
H. mediosora (2) 1 H
H. himalayensis 1 H
H. taeniophylla 1 H
H. taeniophylla 1 H
H. plurisulcata 1 H
H. linearifolia 1 H
H. doniana 1 H
H. fudzinoi 1 H
H. dareicarpa 1 M
H. elongata 1 H
H. elongata 1 H
H. elongata 1 H
H. elongata (2) 1 H
H. elongata (3) 1 H
H. angustifolia (3) 1 H
H. sikkimensis 1 H
H. hainanensis 1 H
H. ensiformis 1 H
H. ensiformis 1 H
H. ensiformis 1 H
H. anguste-elongata 1 H
H. anguste-elongata 1 H
H. alternans (2) 1 H Haplopteris
A. manniana (2) 1 S
A. bivittata 1 S
A. boryana (2) 1 S Antrophyopsis
A. obovatum 3 A
A. castaneum 3 A
A. latifolium 3 A
A. subfalcatum 3 A
A. plantagineum 3 A
A. parvulum (2) 3 A
A. semicostatum (2) 3 A
A. formosanum 3 A
A. henryi 3 A
A. coriaceum 3 A
A. annamense 3 A
A. sessilifolium (2) 3 A
A. malgassicum 3 A
A. vittarioides 3 A
A. wallichianum (2) 3 A
A. reticulatum 3 A
A. callifolium (4) 3 A Antrophyum
P. brasilianum (2) 3 P
P. citrifolium (3) 3 T
P. lineatum (3) 3 P
P. cajenense (2) 3 P
P. guayanense (2) 3 P
P. chlorosporum 3 P
P. feei (2) 3 P Polytaenium
S. ensiformis (2) 1 S Scoliosorus
A. angustifolius (3) 1 N Ananthacorus
V. lineata (4) 1 V
V. bradeorum 3 V
V. lineata 1 V
V. isoetifolia 1 V
V. isoetifolia 1 V
V. graminifolia 3 V
V. graminifolia 3 V
V. scabrida (2) 3 V
V. graminifolia (2) 3 V
V. graminifolia 3 V
V. appalachiana (2) - V Vittaria
1
2
3
4
5
leaf venation
pinnately compound free
indistinct pinnate free
forked free
biseriate areolate
singular free
pluriseriate areolate
parallel free
apical cells of soral paraphyses
spherical
slender
obconic
soral paraphyses absent
spores
3 trilete
1 monolete
- not produced
geographical distribution
Asia and the Pacific Ocean
Americas
Africa and the Indian Ocean
genus sensu Crane (1997)
A Antrophyum
H Haplopteris
I Hecistopteris
M Monogramma
N Ananthacorus
O Rheopteris
P Polytaenium
R Radiovittaria
S Scoliosorus
T Anetium
V Vittaria

resurrection of existing generic or subgeneric (in one instance) names. However, sampling for these early studies was limited to just 23 vittarioid species and, notably, two then-recognized genera (*Monogramma*, *Rheopteris*) were not included. A more recent study of the group (Ruhfel & al., 2008) revealed *Monogramma* to also be polyphyletic, with one element sister to *Rheopteris* and another rendering *Haplopteris* paraphyletic. Nevertheless, this more recent study included only 33 vittarioid species and also relied on a single gene (*rbcL*). Important parts of the family were therefore left out and, although genera (as then sampled) were typically well supported as monophyletic, some generic circumscriptions and relationships remained rather uncertain. The present study, incorporating 72 species (well over half of vittarioid diversity) and many more plastid characters, provides considerable new insight.

Our phylogeny (Figs. 2, 3; Electr. Suppl.: Fig. S1) reveals strong support for the monophyly of *Antrophyum*, *Radiovittaria*, and *Vittaria*, as circumscribed by Crane (1997). Four additional genera in our analysis are either monotypic (*Ananthacorus*, *Anetium*, *Rheopteris*) or represented by a single species (*Hecistopteris*). However, the four remaining genera in Crane's classification (*Haplopteris*, *Monogramma*, *Polytaenium*, *Scoliosorus*) are herein resolved as being either paraphyletic or polyphyletic (Fig. 3).

As in Ruhfel & al. (2008), we find most of *Monogramma* sensu Crane (1997) to be sister to *Rheopteris*, but we here resolve the remainder of the genus in not one, but two different places within *Haplopteris* sensu Crane (1997). Specifically, we resolve an Asian/Pacific Ocean species (*M. dareicarpa* Hook.) within a mostly Asian/Pacific Ocean clade of *Haplopteris*, whereas the African/Indian Ocean species (*M. graminea* (Poir.) Schkuhr, the type of *Monogramma*) is sister to a purely African/Indian Ocean *Haplopteris* clade (Fig. 3). *Scoliosorus* also appears in more than one place in our phylogeny. The American species (*S. ensiformis* (Hook.) T.Moore, the type of *Scoliosorus*) is strongly supported as sister to the monotypic American genus *Ananthacorus*, whereas three African/Indian Ocean species previously placed in *Scoliosorus* form a clade sister to *Antrophyum* (Fig. 3). Finally, we resolve *Polytaenium* as paraphyletic relative to the monotypic *Anetium*.

Taxonomic implications. — It is our opinion that suprageneric taxa ought to be monophyletic, morphologically distinguishable, and stable. Although we understand that many existing taxa (in ferns and in other groups) fail to meet one or more of these criteria, it is our hope that by prioritizing monophyly and then diagnosability in our taxonomic revisions, we can simultaneously accomplish the goal of long-term stability (despite some requisite changes in the short-term). In this taxonomic revision of vittarioid ferns, we recognize only monophyletic genera. We also prioritize diagnosability, but we attempt to strike a balance with stability by minimizing changes relative to earlier classifications. We pay special attention to well-established monotypic genera (of which there are several in the vittarioid fern clade) and consider the merits of maintaining these taxa versus merging them with another genus.

The monotypic *Rheopteris*, with its compound leaves and round sori (Fig. 1E), is unquestionably the least reduced and most distinctive vittarioid element. In this study, we find it to be sister to some of the most reduced species (previously treated in *Monogramma*), to which the name *Vaginularia* has been (and is) applied (see below). Although *Rheopteris* shares some characteristics with this group (e.g., free venation and trilete spores), we see no compelling reason to merge the two genera.

The monotypic *Ananthacorus* is also very distinct, being the only vittarioid genus with pluriseriate areolate venation and sporangia that are restricted to submarginal commissures. Its closest relative (*Scoliosorus ensiformis*), although possessing the same venation and spore type, has differently shaped cells at the apices of its soral paraphyses and sporangia that are not restricted to submarginal commissures. We therefore favor the continued recognition of *Ananthacorus* (as well as *Scoliosorus*; see further discussion below).

Anetium, the third monotypic vittarioid genus following the circumscriptions of Crane (1997), has traditionally been segregated based solely on the presence of sporangia between its leaf veins. But, in all other characters this taxon fits nicely within Crane's (1997) definition of *Polytaenium*. Most notably, these two genera lack paraphyses, which are present in all other vittarioids. In our analysis, we resolve *Anetium* within *Polytaenium* (Fig. 3); convincing support for the paraphyly of *Polytaenium* is not present, but taking into account morphology (and the seemingly impossible task of subdividing *Polytaenium*), we feel the inclusion of *Anetium* within *Polytaenium* is warranted.

Hecistopteris is not monotypic but, to date, only the most common (of three; Moran & Øllgaard, 1995; Kelloff & McKee, 1998) species (*H. pumila* (Spreng.) J.Sm.) has been included in phylogenetic analyses. In our study (as in Ruhfel & al., 2008), it is well supported as sister to *Radiovittaria* (Fig. 3). Although these two genera both have paraphyses with obconic apical cells, this characteristic is also found in *Haplopteris* and some species previously placed in *Monogramma*. Additionally, whereas *Radiovittaria* has biseriate areolate venation and monolete spores, *Hecistopteris* has forked free venation and trilete spores. Thus, we maintain these genera as distinct.

◀ **Fig. 3.** Vittarioid fern phylogeny, with key morphological features and geographical distributions provided for each sampled species. Phylogeny is based on maximum likelihood analysis of a four-gene (*atpA*, *chlN*, *rbcL*, *rpoA*) plastid dataset incorporating 138 ingroup individuals (see Fig. 2). Solid branches in tree received good support (i.e., BS ≥ 70 *and* PP ≥ 0.95); dotted branches were poorly supported (i.e., BS < 70 *or* PP < 0.95). White numbers in black circles at nodes correspond to major clades/subclades discussed in the text. Samples of a given species that shared the same broad distribution were reduced to a single terminal when well supported as monophyletic (number of samples attributed to a particular terminal provided in parentheses, if more than one; see Fig. 2 for non-reduced tree and Fig. S1 [Electr. Suppl.] for support values). Note that species names in tree follow the generic classification proposed herein (to the right of brackets); generic assignments sensu Crane (1997), indicated by letters (to the left of brackets) are provided to facilitate discussion.

Our results also support the continued recognition of *Vittaria* as circumscribed by Crane (1997). This small, mostly American genus is well supported as monophyletic and easily recognized by the combination of biseriate areolate venation and soral paraphyses with slender apical cells.

Monogramma, as circumscribed by Crane (1997), and previously by Kramer (1990), includes those vittarioid species with minute simple leaves having a single vein and sometimes also a few indistinct lateral veins. However, the earliest phylogenetic studies to include members of this genus (Schuettpelz & al., 2007; Ruhfel & al., 2008) indicated that it was polyphyletic, with apparently three independent reductions in morphological complexity. Ruhfel & al. (2008) noted that one distinct element corresponded to (and included the type of) the sometimes segregated genus *Vaginularia* (Lindsay, 2003). Our analysis also favors the recognition of *Vaginularia* and finds it to be strongly supported (BS = 100; PP = 1.00; Figs. 2, 3) as sister to *Rheopteris*. Notably, *Vaginularia* has soral paraphyses with slender apical cells, whereas all other elements previously treated in *Monogramma* sensu Crane (1997) have paraphyses with obconic apical cells. *Vaginularia* can also be distinguished based on its lateral veins, although these are usually indistinct (unless cleared with bleach; Ruhfel & al., 2008).

The second element of *Monogramma* uncovered in the Ruhfel & al. (2008) analysis consisted only of *M. dareicarpa*, which was shown to be firmly embedded in the genus *Haplopteris*. These authors suggested that the type of *Monogramma* (*M. graminea*) was likely also to be resolved here and pointed to the potential need to synonymize *Haplopteris* (the younger name), based on priority, in *Monogramma*. However, Lindsay & Chen (2014) later argued (citing unpublished data) that *M. graminea* is only distantly related to *M. dareicarpa*; the authors thus only provided a new combination for *M. dareicarpa* in *Haplopteris*. As it turns out, published data already existed to suggest that *M. graminea* and *M. dareicarpa* were not closely related. Although the two species had not been analyzed together, their phylogenetic affinities were divergent (Schuettpelz & al., 2007; Ruhfel & al., 2008).

Our analysis (Figs. 2, 3) includes *Monogramma dareicarpa* and *M. graminea* simultaneously for the first time and clearly demonstrates that although both are allied to *Haplopteris*, they occupy rather different phylogenetic positions. The Asian/Pacific Ocean *M. dareicarpa* is closely related to the *H. ensiformis* (Sw.) E.H.Crane and *H. elongata* (Sw.) E.H.Crane groups within a diverse clade of predominantly Asian/Pacific Ocean *Haplopteris* species. The African/Indian Ocean *M. graminea*, on the other hand, is resolved as sister to a smaller, exclusively African/Indian Ocean clade of *Haplopteris* (Fig. 3). These two geographically divergent clades of *Haplopteris*/*Monogramma* also deviate in their typical spore type, with species belonging to the former (Asian/Pacific Ocean) clade generally having monolete spores (*H. malayensis*, with trilete spores, is the exception; Fig. 3), and species belonging to the latter (African/Indian Ocean) clade having trilete spores. However, because neither the geographical nor morphological differences are consistent among these clades, we here favor recognizing them as a single genus. The type of *Haplopteris* (*H. scolopendrina* (Bory) C.Presl) and that of *Monogramma* (*M. graminea*) are both resolved therein (Figs. 2, 3). *Monogramma* is the older name (published in 1809 versus 1836 for *Haplopteris*) and, based simply on the principle of priority, the correct name. That said, the vast majority of the perhaps 40 species in this group are currently treated in *Haplopteris*; only two have ever been placed in *Monogramma*. For the sake of stability, we therefore propose the conservation of *Haplopteris* over *Monogramma* (Chen & al., 2016) and we use *Haplopteris* as the genus name in our figures, key, and list of recognized genera herein. Of course, should our proposal fail, "*Haplopteris*" would need to be replaced with "*Monogramma*" in these instances.

Antrophyum was circumscribed by Crane (1997) to include all Old World vittarioids with pluriseriate areolate venation and trilete spores. Old World vittarioids with pluriseriate areolate venation and monolete spores were treated in *Scoliosorus*. In our analysis, we find strong support (BS = 100; PP = 1.00; Figs. 2, 3) for Crane's (1997) definition of *Antrophyum*. However, the situation is somewhat more complicated for those species previously placed in *Scoliosorus*. We find the only American species of *Scoliosorus* (*S. ensiformis*), which is also the type, to be sister to the American genus *Ananthacorus* (BS = 100; PP = 1.00; Figs. 2, 3). A newly redefined *Scoliosorus* would therefore be monotypic; although *Ananthacorus* is also monotypic, there is little morphological basis for combining it with *Scoliosorus*. The three other species of Crane's (1997) *Scoliosorus* sampled here are all from Africa and the Indian Ocean and they form a well-supported clade (BS = 100; PP = 1.00) that is most closely related to *Antrophyum* (BS = 100; PP = 1.00; Figs. 2, 3). Because these three African/Indian Ocean species differ from *Antrophyum* in having monolete (rather than trilete) spores and also have a disparate distribution (*Antrophyum* is essentially an Asian/Pacific Ocean genus), we feel that genus-level separation is warranted. Here, we place the African/Indian Ocean species in *Antrophyopsis* (Benedict) Schuettp., based on *Antrophyum* subg. *Antrophyopsis* of Benedict (1907).

Taxonomic summary. — In all, we support the recognition of eleven vittarioid genera: *Ananthacorus*, *Antrophyopsis*, *Antrophyum*, *Haplopteris*, *Hecistopteris*, *Polytaenium*, *Radiovittaria*, *Rheopteris*, *Scoliosorus*, *Vaginularia*, and *Vittaria*. Each of these is readily diagnosable based on morphology (see key to genera and brief generic descriptions below), with micromorphological characters related to paraphyses and spores generally complementing more obvious features such as venation and the distribution of sporangia. Compared to the most recent near-comprehensive treatment (Crane, 1997), the circumscriptions of five genera (*Ananthacorus*, *Antrophyum*, *Hecistopteris*, *Radiovittaria*, *Vittaria*) are untouched. *Rheopteris* is simply brought back into consideration. *Anetium* is synonymized here within *Polytaenium* and the latter is thus redefined. Most species previously treated in *Monogramma* are placed in the genus *Vaginularia*; the remaining two (including the type of *Monogramma*) are incorporated into *Haplopteris*. The name *Scoliosorus* is here applied only to the American (type) species, with the African/Indian Ocean species formerly treated in *Scoliosorus* now composing a new genus, *Antrophyopsis*

(Benedict) Schuettp. Below, we provide a key to the currently recognized vittarioid genera, a list of genera including type information and a brief description for each genus, and five new species combinations.

■ TAXONOMY

Key to currently recognized vittarioid fern genera

1. Leaves pinnately compound; sori round; plants of New Guinea …… ***Rheopteris***
1. Leaves simple, forked, or lobed; sori linear (reticulate or not); plants of Africa and the Indian Ocean, the Americas, or Asia and the Pacific Ocean (including New Guinea) 2
2. Leaf venation free (difficult to observe in plants with especially thick or narrow leaves unless cleared with bleach); plants generally diminutive, with leaves typically less than 10 cm long; sori usually appearing as one (continuous or discontinuous) line on each leaf (or each division if leaves forked or lobed) …… 3
2. Leaf venation areolate (difficult to observe in plants with especially thick or narrow leaves unless cleared with bleach); plants generally larger, with leaves typically more than 10 cm long; sori always appearing as two or more lines (reticulate or not) on each leaf (or each division if leaves forked or lobed) …… 6
3. Leaves forked or lobed; plants of the Americas …… …… ***Hecistopteris***
3. Leaves simple; plants of Africa and the Indian Ocean or Asia and the Pacific Ocean …… 4
4. Leaf venation consisting of two or three parallel veins of equal length; apical cells of soral paraphyses spherical .. …… ***Antrophyopsis***
4. Leaf venation consisting of a midrib, with or without 1–3 indistinct lateral veins; apical cells of soral paraphyses slender or obconic …… 5
5. Apical cells of soral paraphyses slender; leaf venation consisting of a midrib and 1–3 indistinct lateral veins; plants of Asia and the Pacific Ocean …… ***Vaginularia***
5. Apical cells of soral paraphyses obconic; leaf venation consisting of a midrib only; plants of Africa and the Indian Ocean or Asia and the Pacific Ocean ……. ***Haplopteris***
6. Leaf venation biseriate areolate, leaves with two rows of areolae (one on each side of midrib); sori restricted to submarginal commissures; leaves most often less than 1 cm wide …… 7
6. Leaf venation pluriseriate areolate, leaves with three or more rows of areolae; sori restricted to submarginal commissures or not; leaves most often more than 1 cm wide …… 9
7. Apical cells of soral paraphyses slender; plants of Africa and the Indian Ocean or the Americas …… ***Vittaria***
7. Apical cells of soral paraphyses obconic; plants of Africa and the Indian Ocean, the Americas, or Asia and the Pacific Ocean …… 8
8. Rhizomes radial, leaf arrangement polystichous; plants of the Americas …… ***Radiovittaria***
8. Rhizomes dorsiventral, leaf arrangement distichous; plants of Africa and the Indian Ocean or Asia and the Pacific Ocean …… ***Haplopteris***
9. Sori restricted to submarginal commissures; plants of the Americas …… ***Ananthacorus***
9. Sori not restricted to submarginal commissures; plants of Africa and the Indian Ocean, the Americas, or Asia and the Pacific Ocean …… 10
10. Soral paraphyses absent; plants of the Americas …… …… ***Polytaenium***
10. Soral paraphyses present; plants of Africa and the Indian Ocean, the Americas, or Asia and the Pacific Ocean .. 11
11. Spores trilete; apical cells of soral paraphyses slender or spherical; plants of Africa and the Indian Ocean or Asia and the Pacific Ocean …… ***Antrophyum***
11. Spores monolete; apical cells of soral paraphyses spherical; plants of Africa and the Indian Ocean or the Americas . 12
12. Leaves costate, midrib present; plants of the Americas .. …… ***Scoliosorus***
12. Leaves ecostate, midrib absent; plants of Africa and the Indian Ocean …… ***Antrophyopsis***

Currently recognized vittarioid fern genera

Ananthacorus Underw. & Maxon in Contr. U.S. Natl. Herb. 10: 487. 1908 – Type: *Ananthacorus angustifolius* (Sw.) Underw. & Maxon (≡ *Pteris angustifolia* Sw.).

Rhizome dorsiventral; leaf arrangement distichous. Leaves simple; costate; venation pluriseriate areolate. Sori linear, restricted to submarginal commissures; soral paraphyses with slender apical cells. Spores monolete.

One species in tropical America.

Antrophyopsis (Benedict) Schuettp., **stat. nov.** ≡ *Antrophyum* subg. *Antrophyopsis* Benedict in Bull. Torrey Bot. Club 34: 447. 1907 – Type: *Antrophyopsis boryana* (Willd.) Schuettp. (≡ *Hemionitis boryana* Willd.).

Rhizome dorsiventral; leaf arrangement distichous. Leaves simple; ecostate; venation pluriseriate areolate or, in one species, free and consisting of 2–3 parallel veins of equal length. Sori linear, along reticulate veins or, in one species with free venation, along the 2–3 parallel veins; soral paraphyses with spherical apical cells. Spores monolete.

Three species in tropical Africa and the Indian Ocean.

Antrophyum Kaulf., Enum. Filic.: 197, 282. 1824 – Lectotype (designated by J.Sm., Hist. Fil. 154. 1875): *Antrophyum plantagineum* (Cav.) Kaulf. (≡ *Hemionitis plantaginea* Cav.).

Rhizome dorsiventral; leaf arrangement distichous. Leaves simple; ecostate or, in a few species, partially costate; venation pluriseriate areolate. Sori linear, along reticulate veins; soral paraphyses with slender or spherical apical cells. Spores trilete.

Perhaps 40 species. Most species in tropical Asia and the Pacific Ocean, but at least one species in tropical Africa and the Indian Ocean.

Haplopteris C.Presl, Tent. Pterid.: 141. 1836 – Type: *Haplopteris scolopendrina* (Bory) C.Presl (≡ *Pteris scolopendrina* Bory).

= *Pleurofossa* Nakai ex H.Ito in J. Jap. Bot. 12: 408. 1936 – Type: *Pleurofossa dareicarpa* (Hook.) Nakai ex H.Ito ("*dareaecarpa*") (≡ *Monogramma dareicarpa* Hook. ("*dareaecarpa*")).

Rhizome dorsiventral; leaf arrangement distichous. Leaves simple or, in a few species, forked; costate; venation biseriate areolate or, in two species, consisting of a single vein. Sori linear, restricted to submarginal commissures or, in two species, along the single vein; soral paraphyses with obconic apical cells. Spores monolete or trilete.

Perhaps 40 species. Most species in tropical Asia and the Pacific Ocean, but about ten species in tropical Africa and the Indian Ocean.

For the sake of stability, we propose the conservation of *Haplopteris* over *Monogramma* Comm. ex Schkuhr (24 Kl. Linn. Pfl.-Syst.: 82. 1809), which, based on the principle of priority, would be the correct name for this group (Chen & al., 2016). We use *Haplopteris* as the genus name here, as well as in our figures and key; should our proposal fail, "*Haplopteris*" would need to be replaced with "*Monogramma*" in these instances.

Hecistopteris J.Sm. in London J. Bot. 1: 193. 1842 – Type: *Hecistopteris pumila* (Spreng.) J.Sm. (≡ *Gymnogramma pumila* Spreng.).

Rhizome dorsiventral; leaf arrangement distichous. Leaves forked or, in one species, lobed; ecostate; venation free, veins forked. Sori linear, along vein ends; soral paraphyses with obconic apical cells. Spores trilete.

Three species in tropical America.

Polytaenium Desv. in Mém. Soc. Linn. Paris 6: 174, 218. 1827 – Type: *Polytaenium lanceolatum* (Sw.) Desv. (≡ *Vittaria lanceolata* Sw.).

= *Anetium* Splitg. in Tijdschr. Natuurl. Gesch. Physiol. 7: 395. 1840 – Type: *Anetium citrifolium* (L.) Splitg. (≡ *Acrostichum citrifolium* L.).

Rhizome dorsiventral; leaf arrangement distichous. Leaves simple; costate; venation pluriseriate areolate. Sori linear, along reticulate veins and, in one species, sporangia also scattered between veins; soral paraphyses absent. Spores trilete.

About ten species in tropical America.

Radiovittaria (Benedict) E.H.Crane in Syst. Bot. 22: 514–515. 1998 ("1997") ≡ *Vittaria* subg. *Radiovittaria* Benedict in Bull. Torrey Bot. Club 38: 166. 1911 – Type: *Radiovittaria remota* (Fée) E.H.Crane (≡ *Vittaria remota* Fée).

Rhizome radial; leaf arrangement polystichous. Leaves simple; costate; venation biseriate areolate. Sori linear, restricted to submarginal commissures; soral paraphyses with obconic apical cells. Spores monolete.

About ten species in tropical America.

Rheopteris Alston in Nova Guinea, n.s., 7: 2. 1956 – Type: *Rheopteris cheesmaniae* Alston.

Rhizome dorsiventral; leaf arrangement distichous. Leaves pinnately compound; pinnae ecostate; venation free, veins forked. Sori round, at vein ends; soral paraphyses with spherical apical cells. Spores trilete.

One species in New Guinea.

Scoliosorus T.Moore, Index Fil.: xxix. 1857 – Type: *Scoliosorus ensiformis* (Hook.) T.Moore (≡ *Antrophyum ensiforme* Hook.).

Rhizome dorsiventral; leaf arrangement distichous. Leaves simple; costate; venation pluriseriate areolate. Sori linear, along reticulate veins; soral paraphyses with spherical apical cells. Spores monolete.

One species in tropical America.

Vaginularia Fée, Mém. Foug. 3: 30–31. 1852 – Type: *Vaginularia trichoidea* Fée.

= *Diclidopteris* Brack., U.S. Expl. Exped., Filic. [= in Wilkes, U.S. Expl. Exped. 16]: 135. 1854 – Type: *Diclidopteris angustissima* Brack.

Rhizome dorsiventral; leaf arrangement distichous. Leaves simple; costate; venation free, consisting of a midrib and 1–3 indistinct lateral veins. Sori linear, along lateral veins, usually appearing as one (continuous or discontinuous) line; soral paraphyses with slender apical cells. Spores trilete.

Four species in tropical Asia and the Pacific Ocean.

Vittaria Sm. in Mém. Acad. Roy. Sci. (Turin) 5: 413, t. 9, fig. 5. 1793 – Type: *Vittaria lineata* (L.) Sm. (≡ *Pteris lineata* L.).

Rhizome dorsiventral; leaf arrangement distichous. Leaves simple; costate; venation biseriate areolate. Sori linear, restricted to submarginal commissures; soral paraphyses with slender apical cells. Spores monolete or trilete.

Seven species. Most species in tropical America, but one in tropical Africa and the Indian Ocean and one restricted to temperate North America.

New combinations

Antrophyopsis bivittata (C.Chr.) Schuettp., **comb. nov.** ≡ *Antrophyum bivittatum* C.Chr. in Bonaparte, Notes Ptéridol. 16: 110, pl. 1. 1925.

Antrophyopsis boryana (Willd.) Schuettp., **comb. nov.** ≡ *Hemionitis boryana* Willd., Sp. Pl. 5(1): 128. 1810 ≡ *Antrophyum boryanum* (Willd.) Spreng., Syst. Veg. 4(1): 67. 1827 ≡ *Scoliosorus boryanus* (Willd.) E.H.Crane in Syst. Bot. 22: 515. 1998 ("1998") ("*boryanum*").

Antrophyopsis manniana (Hook.) Schuettp., **comb. nov.** ≡ *Antrophyum mannianum* Hook., Sec. Cent. Ferns: t. 73. 1861 ≡ *Scoliosorus mannianus* (Hook.) E.H.Crane in Syst. Bot. 22: 515. 1998 ("1997") ("*mannianum*").

Haplopteris schliebenii (Reimers) Schuettp., **comb. nov.** ≡ *Vittaria schliebenii* Reimers in Notizbl. Bot. Gart. Berlin-Dahlem 11: 924. 1933.

Polytaenium citrifolium (L.) Schuettp., **comb. nov.** ≡ *Acrostichum citrifolium* L., Sp. Pl.: 1067. 1753 ≡ *Anetium citrifolium* (L.) Splitg. in Tijdschr. Natuurl. Gesch. Physiol 7: 395. 1840 ≡ *Antrophyum citrifolium* (L.) Fée, Mém. Foug. 4: 51. 1852 ≡ *Hemionitis citrifolia* (L.) Hook., Sp. Fil. 5: 193. 1864 ≡ *Pteridanetium citrifolium* (L.) Copel., Gen. Fil.: 224. 1947.

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Appendix 1. Individuals sampled in this study of vittarioid ferns. For each individual, the species name, Fern Lab Database (http://fernlab.biology.duke.edu) voucher number, voucher information, place of origin, and GenBank accession numbers (*atpA*, *chlN*, *rbcL*, *rpoA*) are provided. An n-dash (–) indicates unavailable information; new sequences are prefixed with KX.

Adiantum andicola Liebm., **5549**, *C.J. Rothfels 2641* (DUKE), Costa Rica (San José), KU147243, KU147251, KU147272, KU147280; ***Adiantum capillus-veneris*** L., **4609**, *L. Huiet 104* (UC), United States (California), KU147244, KU147252, KU147273, KU147281; ***Adiantum formosum*** R.Br., **4602**, *A.R. Smith s.n.* (UC), Cultivated (–), KC984437, KU147257, KC984520, KU147289; ***Adiantum malesianum*** J.Ghatak, **2506**, *L. Huiet 111* (UC), Cultivated (–), KX165157, KU147258, EF452132, KU147291; ***Adiantum peruvianum*** Klotzsch, **2507**, *L. Huiet 103* (UC), Cultivated (–), KX165158, KU147259, EF452133, KU147292; ***Adiantum tenerum*** Sw., **2504**, *L. Huiet 107* (UC), Cultivated (–), KX165159, KU147260, EF452134, KU147294; ***Adiantum tetraphyllum*** Humb. & Bonpl. ex Willd., **2505**, *L. Huiet 105* (UC), Cultivated (–), EF452073, KU147261, EF452135, KU147295; ***Ananthacorus angustifolius*** (Sw.) Underw. & Maxon, **5271**, *F. Matos 08-203* (DUKE), Costa Rica (Heredia), KU517449, KU517485, KU517577, KU517613; ***Ananthacorus angustifolius*** (Sw.) Underw. & Maxon, **9376**, *A. Garrido 2113* (MO), Nicaragua (Río San Juan), KX165160, –, KX164950, –; ***Ananthacorus angustifolius*** (Sw.) Underw. & Maxon, **9704**, *P.M. Peterson 6384* (US), Panama (Bocas del Toro), KX165161, KX165063, KX164951, KX164853; ***Antrophyopsis bivittata*** (C.Chr.) Schuettp., **9396**, *J. Rabenantoandro 521* (MO), Madagascar (Antsiranana), KX165162, –, KX164952, –; ***Antrophyopsis boryana*** (Willd.) Schuettp., **9076**, *J. Kluge 8047* (UC), Madagascar (Sava), KX165246, KX165064, KX164953, KX164854; ***Antrophyopsis boryana*** (Willd.) Schuettp., **9703**, *J.S. Miller 3534* (US), Madagascar (Antsiranana), KX165163, KX165065, KX164954, KX164855; ***Antrophyopsis manniana*** (Hook.) Schuettp., **9401**, *L. Festo 2008* (MO), Tanzania (Iringa), KX165164, KX165066, KX164955, KX164856; ***Antrophyopsis manniana*** (Hook.) Schuettp., **9702**, *I. Friis 11983* (US), Ethiopia (–), KX165165, KX165067, KX164956, KX164857; ***Antrophyum annamense*** Tardieu & C.Chr., **9391**, *S.K. Wu 96* (MO), Laos (Kouankhanh), KX165172, KX165073, KX164963, KX164863; ***Antrophyum annamense*** Tardieu & C.Chr., **9673**, *W.H. Wu 956* (TAIF), China (Hainan), KX165166, KX165068, KX164957, KX164858; ***Antrophyum callifolium*** Blume, **4081**, *E. Schuettpelz 668* (DUKE), Malaysia (Selangor), KX165167, KX165069, KX164958, KX164859; ***Antrophyum callifolium*** Blume, **9018**, *D. Karger 875* (UC), Indonesia (Sulawesi), KX165168, KX165070, KX164959, KX164860; ***Antrophyum callifolium*** Blume, **9393**, *W. Sugong 1826* (MO), Laos (Saraven), KX165169, –, KX164960, –; ***Antrophyum callifolium*** Blume, **9674**, *C.W. Chen SITW0065* (TAIF), Solomon Islands (Guadalcanal), KX165170, KX165071, KX164961, KX164861; ***Antrophyum castaneum*** H.Ito, **9675**, *C.W. Chen 375* (TAIF), Taiwan (Hsinchu), KX165171, KX165072, KX164962, KX164862; ***Antrophyum formosanum*** Hieron., **8409**, *T. Ranker 2068* (COLO), Taiwan (Taipei), KU517451, KU517487, KU517579, KU517615; ***Antrophyum henryi*** Hieron., **9677**, *L.Y. Kuo 3314* (TAIF), China (Yunnan), KX165173, KX165074, KX164964, KX164864; ***Antrophyum latifolium*** Blume, **3078**, *T. Ranker 1774* (COLO), Papua New Guinea (–), KX165174, KU147263, EF452138, KU147297; ***Antrophyum malgassicum*** C.Chr., **9398**, *F. Rakotondrainibe 1730* (MO), Madagascar (Antsiranana), KX165175, –, KX164965, –; ***Antrophyum obovatum*** Baker, **8412**, *T. Ranker 2082* (COLO), Taiwan (Nantou), KX165176, KX165075, KX164966, KX164865; ***Antrophyum parvulum*** Blume, **9030**, *D. Karger 1333* (UC), Indonesia (Lombok), KX165247, KX165076, KX164967, KX164866; ***Antrophyum parvulum*** Blume, **9679**, *C.W. Chen 2212* (TAIF), Taiwan (Chiayi), KX165177, KX165077, KX164968, KX164867; ***Antrophyum plantagineum*** (Cav.) Kaulf., **9680**, *C.W. Chen SITW01128* (TAIF), Solomon Islands (Western), KX165178, KX165078, KX164969, KX164868; ***Antrophyum reticulatum*** (G.Forst.) Kaulf., **8414**, *T. Ranker 1948* (COLO), French Polynesia (Moorea), KX165179, KX165079, KX164970, KX164869; ***Antrophyum semicostatum*** Blume, **8415**, *T. Ranker 2162* (SAN), Malaysia (Sabah), KX165180, KX165080, KX164971, KX164870; ***Antrophyum semicostatum*** Blume , **9066**, *J. Kluge 7135* (UC), Indonesia (Sulawesi), KX165248, KX165081, KX164972, KX164871; ***Antrophyum sessilifolium*** (Cav.) Spreng., **8999**, *D. Cicuzza 927* (UC), Indonesia (Sulawesi), KX165249, KX165082, KX164973, KX164872; ***Antrophyum sessilifolium*** (Cav.) Spreng., **9681**, *C.W. Chen 1502* (TAIF), Taiwan (Taitung), KX165181, KX165083, KX164974, KX164873; ***Antrophyum subfalcatum*** Brack., **9682**, *C.W. Chen SITW1130* (TAIF), Solomon Islands (Western), KX165182, KX165084, KX164975, KX164874; ***Antrophyum vittarioides*** Baker, **9683**, *Lao 0308021* (TAIF), China (Guangxi), KX165183, KX165085, KX164976, KX164875; ***Antrophyum wallichianum*** M.G.Gilbert & X.C.Zhang, **9395**, *W. Sugong 2585* (MO), Laos (Louangphrabang), KX165184, KX165086, KX164977, KX164876; ***Antrophyum wallichianum*** M.G.Gilbert & X.C.Zhang, **9676**, *C.R. Fraser-Jenkins FN12* (TAIF), Nepal (–), KX165185, KX165087, KX164978, KX164877; ***Haplopteris alternans*** (Copel.) S.Linds. & C.W.Chen, **9014**, *D. Karger 685* (UC), Philippines (–), KX165186, KX165088, KX164979, KX164878; ***Haplopteris alternans*** (Copel.) S.Linds. & C.W.Chen, **9034**, *D. Karger 1508* (UC), Philippines (Bukiknon), KX165156, KX165089, KX164980, KX164879; ***Haplopteris amboinensis*** (Fée) X.C.Zhang, **9373**, *Wuzhishan Fern Survey 223* (MO), China (Hainan), KX165187, KX165090, KX164981, –; ***Haplopteris amboinensis*** (Fée) X.C.Zhang, **9684**, *C.W. Chen 2588* (TAIF), Vietnam (Lam Dong), KX165188, KX165091, KX164982, KX164880; ***Haplopteris anguste-elongata*** (Hayata) E.H.Crane, **8407**, *T. Ranker 2012* (COLO), Taiwan (Ilan), KX165250, KX165092, KX164983, KX164881; ***Haplopteris anguste-elongata*** (Hayata) E.H.Crane, **9685**,

Appendix 1. Continued.

C.W. Chen 1482 (TAIF), Taiwan (Taipei), KX165189, KX165093, KX164984, KX164882; ***Haplopteris angustifolia*** (Blume) E.H.Crane, **8997**, *D. Cicuzza 818* (UC), Indonesia (Sulawesi), KX165251, KX165094, KX164985, KX164883; ***Haplopteris angustifolia*** (Blume) E.H.Crane, **9092**, *M. Kessler 13631* (UC), Malaysia (–), KX165190, KX165095, KX164986, KX164884; ***Haplopteris angustifolia*** (Blume) E.H.Crane, **9369**, *Wuzhishan Fern Survey 236* (MO), China (Hainan), KX165191, KX165096, KX164987, KX164885; ***Haplopteris dareicarpa*** (Hook.) S.Linds. & C.W.Chen, **10159**, *P.J. Darbyshire 8032* (US), Papua New Guinea (–), KX165192, KX165097, KX164988, KX164886; ***Haplopteris doniana*** (Mett. ex Hieron.) E.H.Crane, **9686**, *C.W. Chen 2680* (TAIF), Vietnam (Lam Dong), KX165193, KX165098, KX164989, KX164887; ***Haplopteris elongata*** (Sw.) E.H.Crane, **8423**, *T. Ranker 1931* (COLO), French Polynesia (Moorea), KX165194, KX165099, KX164990, KX164888; ***Haplopteris elongata*** (Sw.) E.H.Crane, **9001**, *D. Cicuzza 977* (Z), Indonesia (Sulawesi), KX165252, KX165100, KX164991, KX164889; ***Haplopteris elongata*** (Sw.) E.H.Crane, **9070**, *J. Kluge 7677A* (UC), Comoros (Grand Comore), KX165195, KX165101, KX164992, KX164890; ***Haplopteris elongata*** (Sw.) E.H.Crane, **9075**, *J. Kluge 7865* (UC), Madagascar (–), KX165253, KX165102, KX164993, KX164891; ***Haplopteris elongata*** (Sw.) E.H.Crane, **9093**, *M. Kessler 13632* (UC), Malaysia (–), KX165254, KX165103, KX164994, KX164892; ***Haplopteris elongata*** (Sw.) E.H.Crane, **9363**, *S.K. Wu 394* (MO), Laos (Vientiane), KX165196, KX165104, KX164995, –; ***Haplopteris elongata*** (Sw.) E.H.Crane, **9368**, *Wuzhishan Fern Survey 216* (MO), China (Hainan), –, –, KX164996, –; ***Haplopteris elongata*** (Sw.) E.H.Crane, **9370**, *S.K. Wu 864* (MO), Vietnam (Ha Giang), KX165197, KX165105, KX164997, KX164893; ***Haplopteris ensiformis*** (Sw.) E.H.Crane, **9007**, *D. Karger 311* (UC), Philippines (Bukiknon), KX165198, KX165106, KX164998, –; ***Haplopteris ensiformis*** (Sw.) E.H.Crane, **9023**, *D. Karger 1140* (UC), Indonesia (Seram), –, –, KX164999, –; ***Haplopteris ensiformis*** (Sw.) E.H.Crane, **9343**, *H. van der Werff 12768* (MO), Madagascar (Toamasina), KX165199, KX165107, KX165000, –; ***Haplopteris flexuosa*** (Fée) E.H.Crane, **4786**, *E. Schuettpelz 1043A* (DUKE), Taiwan (Nantou), KX165255, KX165108, KX165001, KX164894; ***Haplopteris flexuosa*** (Fée) E.H.Crane, **9688**, *L.Y. Kuo 3265* (TAIF), China (Yunnan), KX165200, KX165109, KX165002, KX164895; ***Haplopteris fudzinoi*** (Makino) E.H.Crane, **9689**, *L.Y. Kuo 2225* (TAIF), China (Sichuan), KX165201, KX165110, KX165003, KX164896; ***Haplopteris graminea*** (Poir.) comb. ined. (= *Monogramma graminea* (Poir.) Schkuhr), **3548**, *T. Janssen 2692* (P), France (Reunion), KX165202, KU147268, EF452157, KU147304; ***Haplopteris graminea*** (Poir.) comb. ined. (= *Monogramma graminea* (Poir.) Schkuhr), **10158**, *G. Rouhan 1143* (P), Madagascar (–), –, –, KX165004, –; ***Haplopteris guineensis*** (Desv.) E.H.Crane, **9359**, *W. Kindeketa 850* (MO), Tanzania (Kilimanjaro), KX165203, KX165111, KX165005, KX164897; ***Haplopteris guineensis*** (Desv.) E.H.Crane, **9360**, *R. Pérez Viso 3723* (MO), Equatorial Guinea (Wele-Nzas), KX165204, KX165112, KX165006, KX164898; ***Haplopteris hainanensis*** (C.Christensen ex Ching) E.H.Crane, **9690**, *W.H. Wu 959* (TAIF), China (Hainan), KX165205, KX165113, KX165007, KX164899; ***Haplopteris heterophylla*** C.W.Chen, Y.H.Chang & Y.C.Liu, **9691**, *W.H. Wu 1038* (TAIF), China (Hainan), KX165206, KX165114, KX165008, KX164900; ***Haplopteris himalayensis*** (Ching) E.H.Crane, **9692**, *C.R. Fraser-Jenkins 30640* (TAIF), Nepal (–), –, –, KX165009, KX164901; ***Haplopteris humblotii*** (Hieron.) S.Linds. & C.W.Chen, **9345**, *P. Antilahimena 3177* (MO), Madagascar (Toamasina), KX165207, KX165115, KX165010, KX164902; ***Haplopteris humblotii*** (Hieron.) S.Linds. & C.W.Chen, **9346**, *F. Rakotondrainibe 3554* (MO), Madagascar (Antsiranana), KX165208, –, KX165011, –; ***Haplopteris linearifolia*** (Ching) X.C.Zhang, **9693**, *Y.C. Liu 9457* (TAIF), China (Sichuan), KX165209, KX165116, KX165012, KX164903; ***Haplopteris malayensis*** (Holttum) E.H.Crane, **4143**, *E. Schuettpelz 728* (DUKE), Malaysia (Pahang), KX165256, KX165117, KX165013, KX164904; ***Haplopteris mediosora*** (Hayata) X.C.Zhang, **9694**, *C.R. Fraser-Jenkins FN133* (TAIF), Nepal (–), KX165210, KX165118, KX165014, KX164905; ***Haplopteris mediosora*** (Hayata) X.C.Zhang, **9695**, *C.W. Chen 1492* (TAIF), Taiwan (Nantou), KX165211, KX165119, KX165015, KX164906; ***Haplopteris plurisulcata*** (Ching) X.C.Zhang, **9696**, *Z.R. He 2013001* (TAIF), China (Yunnan), KX165212, KX165120, KX165016, KX164907; ***Haplopteris schliebenii*** (Reimers) Schuettp., **9407**, *W. R.Q. Luke 11355* (MO), Tanzania (Iringa), KX165213, KX165121, KX165017, KX164908; ***Haplopteris scolopendrina*** (Bory) C.Presl, **9035**, *D. Karger 1510* (UC), Philippines (Bukiknon), –, –, KX165018, –; ***Haplopteris scolopendrina*** (Bory) C.Presl, **9063**, *J. Kluge 7052* (GOET), Indonesia (Sulawesi), KX165257, KX165122, KX165019, KX164909; ***Haplopteris scolopendrina*** (Bory) C.Presl, **9697**, *C.W. Chen SITW1047* (TAIF), Solomon Islands (Western), KX165214, –, –, KX164910; ***Haplopteris sikkimensis*** (Kuhn) E.H.Crane, **9698**, *C.R. Fraser-Jenkins 30779* (TAIF), Nepal (–), KX165215, –, KX165020, –; ***Haplopteris taeniophylla*** (Copel.) E.H.Crane, **4898**, *E. Schuettpelz 1155A* (DUKE), Taiwan (Taichung), KX165258, KX165123, KX165021, KX164911; ***Haplopteris taeniophylla*** (Copel.) E.H.Crane, **8869**, *F.W. Li 1440* (DUKE), Taiwan (Nantou), KX165216, KX165124, KX165022, KX164912; ***Haplopteris volkensii*** (Hieron.) E.H.Crane, **9341**, *L. Festo 1937* (MO), Tanzania (Morogoro), KX165217, KX165125, KX165023, –; ***Hecistopteris pumila*** (Spreng.) J.Sm., **3278**, *M. J.M. Christenhusz 3976* (TUR), Guadeloupe (Sofaia), EF452097, KU147266, KC984524, KU147303; ***Hecistopteris pumila*** (Spreng.) J.Sm., **5135**, *F. Matos 08-198* (DUKE), Costa Rica (Heredia), KX165218, KX165126, KX165024, KX164913; ***Polytaenium brasilianum*** (Desv.) Benedict, **9087**, *M. Kessler 12940* (UC), Bolivia (Cochabamba), KX165219, KX165127, KX165025, KX164914; ***Polytaenium brasilianum*** (Desv.) Benedict, **9090**, *M. Kessler 13351* (UC), Bolivia (Cochabamba), KX165220, KX165128, KX165026, KX164915; ***Polytaenium cajenense*** (Desv.) Benedict, **2379**, *E. Schuettpelz 211* (DUKE), Ecuador (Napo), KX165259, KX165129, KX165027, KX164916; ***Polytaenium cajenense*** (Desv.) Benedict, **9106**, *P. Weigelt 90365* (LPB), Bolivia (La Paz), KX165221, KX165130, KX165028, KX164917; ***Polytaenium chlorosporum*** (Mickel & Beitel) E.H.Crane, **5147**, *C.J. Rothfels 08-105* (DUKE), Costa Rica (Puntarenas), KX165260, KX165131, KX165029, KX164918; ***Polytaenium citrifolium*** (L.) Schuettp., **3339**, *M. J.M. Christenhusz 4076* (TUR), Guadeloupe (–), EF452075, KU147262, KC984523, KU147296; ***Polytaenium citrifolium*** (L.) Schuettp., **5131**, *C.J. Rothfels 08-188* (DUKE), Costa Rica (Heredia), KX165222, KX165132, KX165030, KX164919; ***Polytaenium citrifolium*** (L.) Schuettp., **9061**, *I. Jiménez 2007* (UC), Bolivia (Pando), KU517450, –, KU517578, KU517614; ***Polytaenium feei*** (W.Schaffn. ex Fée) Maxon, **3258**, *M. J.M. Christenhusz 3951* (TUR), Guadeloupe (Sofaia), KX165261, –, KX165031, KX164920; ***Polytaenium feei*** (W.Schaffn. ex Fée) Maxon, **5148**, *C.J. Rothfels 08-179* (DUKE), Costa Rica (Heredia), KX165223, –, KX165032, KX164921; ***Polytaenium guayanense*** (Hieron.) Alston, **9103**, *P. Weigelt 90073* (LPB), Bolivia (Cochabamba), KX165224, KX165133, KX165033, KX164922; ***Polytaenium guayanense*** (Hieron.) Alston, **9104**, *P. Weigelt 90141* (LPB), Bolivia (Cochabamba), KX165225, KX165134, KX165034, KX164923; ***Polytaenium lineatum*** (Sw.) J.Sm., **5150**, *K.M. Pryer 08-097* (DUKE), Costa Rica (Puntarenas), KX165226, KX165135, KX165035, KX164924; ***Polytaenium lineatum*** (Sw.) J.Sm., **8375**, *E. Schuettpelz 1440* (SP), Brazil (Rio de Janeiro), KU517452, KU517488, KU517580, KU517616; ***Polytaenium lineatum*** (Sw.) J.Sm., **9062**, *I. Jiménez 2393* (UC), Bolivia (Tarija), KX165227, KX165136, KX165036, KX164925; ***Radiovittaria gardneriana*** (Fée) E.H.Crane, **4415**, *E. Schuettpelz 929* (DUKE), Ecuador (Napo), KX165228, KX165137, KX165037, KX164926; ***Radiovittaria gardneriana*** (Fée) E.H.Crane, **8370**, *E. Schuettpelz 1436* (SP), Brazil (Rio de Janeiro), –, KX165138, KX165038, KX164927; ***Radiovittaria gardneriana*** (Fée) E.H.Crane, **9051**, *I. Jiménez 903* (LPB), Bolivia (La Paz), KX165229, KX165139, KX165039, KX164928; ***Radiovittaria latifolia*** (Benedict) E.H.Crane, **9052**, *I. Jiménez 1069* (UC), Bolivia (La Paz), KX165230, KX165140, KX165040, KX164929; ***Radiovittaria latifolia*** (Benedict) E.H.Crane, **9058**, *I. Jiménez 1525* (UC), Bolivia (Cochabamba), KX165231, KX165141, KX165041, KX164930; ***Radiovittaria minima*** (Baker) E.H.Crane, **8553**, *J. Nitta 806* (UC), Costa Rica (Alajuela), KX165232, KX165142, KX165042, KX164931; ***Radiovittaria moritziana*** (Mett.) E.H.Crane, **9046**, *I. Jiménez 689* (UC), Bolivia (La Paz), KX165233, KX165143, KX165043, KX164932; ***Radiovittaria moritziana*** (Mett.) E.H.Crane, **9059**, *I. Jiménez 1606* (UC), Bolivia (Cochabamba), KX165234, KX165144, KX165044, KX164933; ***Radiovittaria remota*** (Fée) E.H.Crane, **8534**, *J. Nitta 732* (UC), Costa Rica (Alajuela), –, KX165145, –, KX164934; ***Radiovittaria ruiziana*** (Fée) E.H.Crane, **9377**, *J.P. Altamirano 513* (MO), Bolivia (Cochabamba), KX165235, KX165146, KX165045, KX164935; ***Radiovittaria ruiziana*** (Fée) E.H.Crane, **9379**, *R. Núnez 318* (MO), Bolivia (Santa Cruz), KX165236, KX165147, KX165046, KX164936; ***Radiovittaria stipitata*** (Kunze) E.H.Crane, **2419**, *E. Schuettpelz 251* (DUKE), Ecuador (Zamora-Chinchipe), KX165237, KX165148, KX165047, KX164937; ***Radiovittaria stipitata*** (Kunze) E.H.Crane, **5153**, *C.J. Rothfels 08-176* (DUKE), Costa Rica (Heredia), KX165238, KX165149, KX165048, KX164938; ***Radiovittaria stipitata*** (Kunze) E.H.Crane, **9045**, *H. Huaylla 1400* (UC), Bolivia (Cochabamba), KX165239, KX165150, KX165049, KX164939; ***Rheopteris cheesmaniae*** Alston, **3373**, *J.R. Croft 1749* (A), Papua New Guinea (–), EF452126, KU147270, EF452176, KU147301; ***Scoliosorus ensiformis*** (Hook.) T.Moore, **6020**, *M. Sundue 1676* (DUKE), Costa Rica (Alajuela), KU517453, KU517489, KU517581, KU517617; ***Scoliosorus ensiformis*** (Hook.) T.Moore, **6652**, *C.J. Rothfels 3254* (DUKE), Mexico (Guerrero), KX165240, KX165151, KX165050, KX164940; ***Vaginularia acrocarpa*** Holttum, **3375**, *T. Ranker 1778* (COLO), Papua New Guinea (–), KC984435, –, EF452156, –; ***Vaginularia acrocarpa*** Holttum, **9005**, *D. Karger 220* (UC), Philippines (–), KX165262, –, KX165051, –; ***Vaginularia acrocarpa*** Holttum, **9100**, *M. Kessler 14254* (Z), Australia (Queensland), KX165263, –, KX165052, –; ***Vaginularia angustissima*** (Brack.) Mett., **9705**, *A.C. Smith 5806* (US), Fiji (–), KX165241, –, KX165053, KX164941; ***Vaginularia paradoxa*** (Fée) Mett. ex Miq., **9036**, *D. Karger 1548* (UC), Philippines (Bukiknon), KX165264,

Appendix 1. Continued.

–, KX165054, KX164942; ***Vaginularia paradoxa*** (Fée) Mett. ex Miq., **9699**, *C.W. Chen 1643* (TAIF), Taiwan (Taitung), KX165242, –, KX165055, KX164943; ***Vaginularia trichoidea*** Fée, **4668**, *F.C. Hou 73143* (UC), China (Hainan), KX165243, –, KX165056, KX164944; ***Vaginularia trichoidea*** Fée, **9091**, *M. Kessler 13601* (UC), Malaysia (–), KX165265, –, KX165057, KX164945; ***Vittaria appalachiana*** Farrar & Mickel, **9229**, *E. Schuettpelz 1482* (WNC), United States (North Carolina), KU517454, KU517490, KU517582, KU517618; ***Vittaria appalachiana*** Farrar & Mickel, **9334**, *S. Stevens NY-p5s2* (PUL), United States (New York), KU517460, KU517495, KU517588, KU517624; ***Vittaria bradeorum*** Rosenst., **8559**, *J. Nitta 834* (UC), Costa Rica (Alajuela), KU517472, KU517507, KU517600, KU517636; ***Vittaria graminifolia*** Kaulf., **2395**, *E. Schuettpelz 227* (DUKE), Ecuador (Zamora-Chinchipe), EF452128, KU147271, KU147279, KU147302; ***Vittaria graminifolia*** Kaulf., **5154**, *C.J. Rothfels 08-106* (DUKE), Costa Rica (Puntarenas), KX165266, KX165152, KX165058, KX164946; ***Vittaria graminifolia*** Kaulf., **8381**, *E. Schuettpelz 1446* (SP), Brazil (Rio de Janeiro), KU517475, KU517510, KU517603, KU517639; ***Vittaria graminifolia*** Kaulf., **9049**, *I. Jiménez 867* (LPB), Bolivia (La Paz), KX165244, KX165153, KX165059, KX164947; ***Vittaria graminifolia*** Kaulf., **9355**, *A. Reyes-García 7120* (MO), Mexico (Chiapas), KX165245, KX165154, KX165060, KX164948; ***Vittaria isoetifolia*** Bory, **9342**, *F. Rakotondrainibe 3202* (MO), Madagascar (Fort Dauphin), –, KU517513, KU517606, KU517642; ***Vittaria isoetifolia*** Bory, **10161**, *T. Janssen 2920* (MO), Madagascar (–), KU517478, KU517514, –, KU517643; ***Vittaria lineata*** (L.) Sm., **5289**, *C.J. Rothfels 08-177* (DUKE), Costa Rica (Heredia), KU517479, KU517515, KU517607, KU517644; ***Vittaria lineata*** (L.) Sm., **8129**, *C.J. Rothfels 4008* (DUKE), United States (Florida), KU517480, KU517516, KU517608, KU517645; ***Vittaria lineata*** (L.) Sm., **8927**, *J. Prado 2248* (SP), Brazil (Sao Paulo), KX165267, KX165155, KX165061, KX164949; ***Vittaria lineata*** (L.) Sm., **9339**, *D.E. Atha 1110* (MO), Belize (Cayo), –, –, KX165062, –; ***Vittaria lineata*** (L.) Sm., **9340**, *G. McPherson 20973* (MO), Panama (–), KU517482, KU517518, KU517610, KU517647; ***Vittaria scabrida*** Klotzsch ex Fée, **8915**, *J. Prado 2249* (SP), Brazil (Sao Paulo), KU517483, KU517519, KU517611, KU517648; ***Vittaria scabrida*** Klotzsch ex Fée, **8925**, *J. Prado 2263b* (SP), Brazil (Sao Paulo), KU517484, KU517520, KU517612, KU517649.

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A revised generic classification of vittarioid ferns (Pteridaceae) based on molecular, micromorphological, and geographic data

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***Taxon* 65: 708–722**

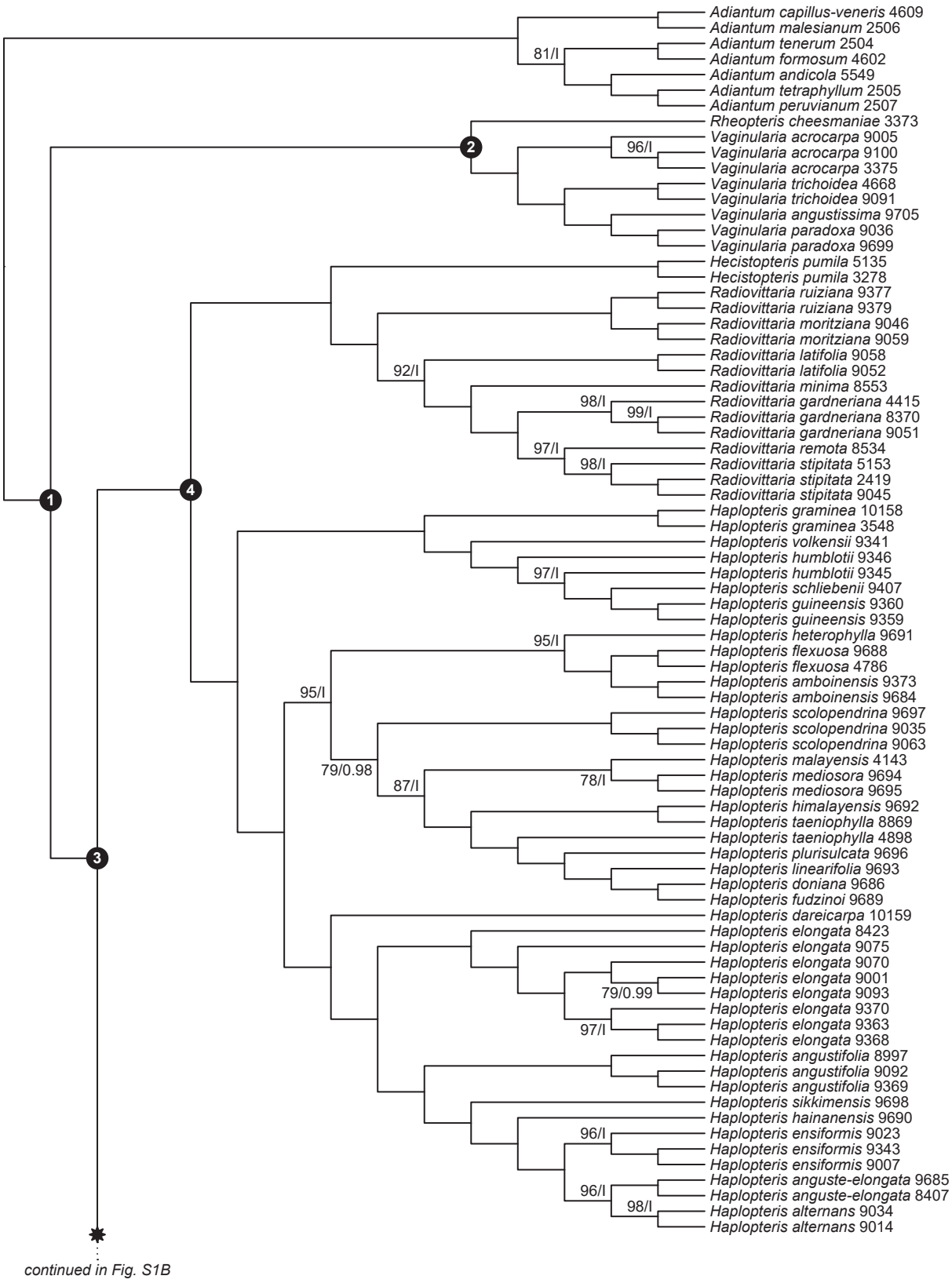

Fig. S1A. Vittarioid fern phylogeny resulting from maximum likelihood analysis of a four-gene (*atpA*, *chlN*, *rbcL*, and *rpoA*) plastid dataset incorporating 138 ingroup and 7 outgroup individuals. Maximum likelihood bootstrap percentages (BS) and Bayesian posterior probabilities (PP) are provided at each node (BS/PP; C = 100; I = 1.00; < = BS < 50 or PP < 0.50). White numbers in black circles at nodes correspond to major clades/subclades discussed in the text. Species names in tree follow the generic classification proposed in this study; numbers following names are Fern Lab Database (http://fernlab.biology.duke.edu) voucher numbers (Appendix 1).

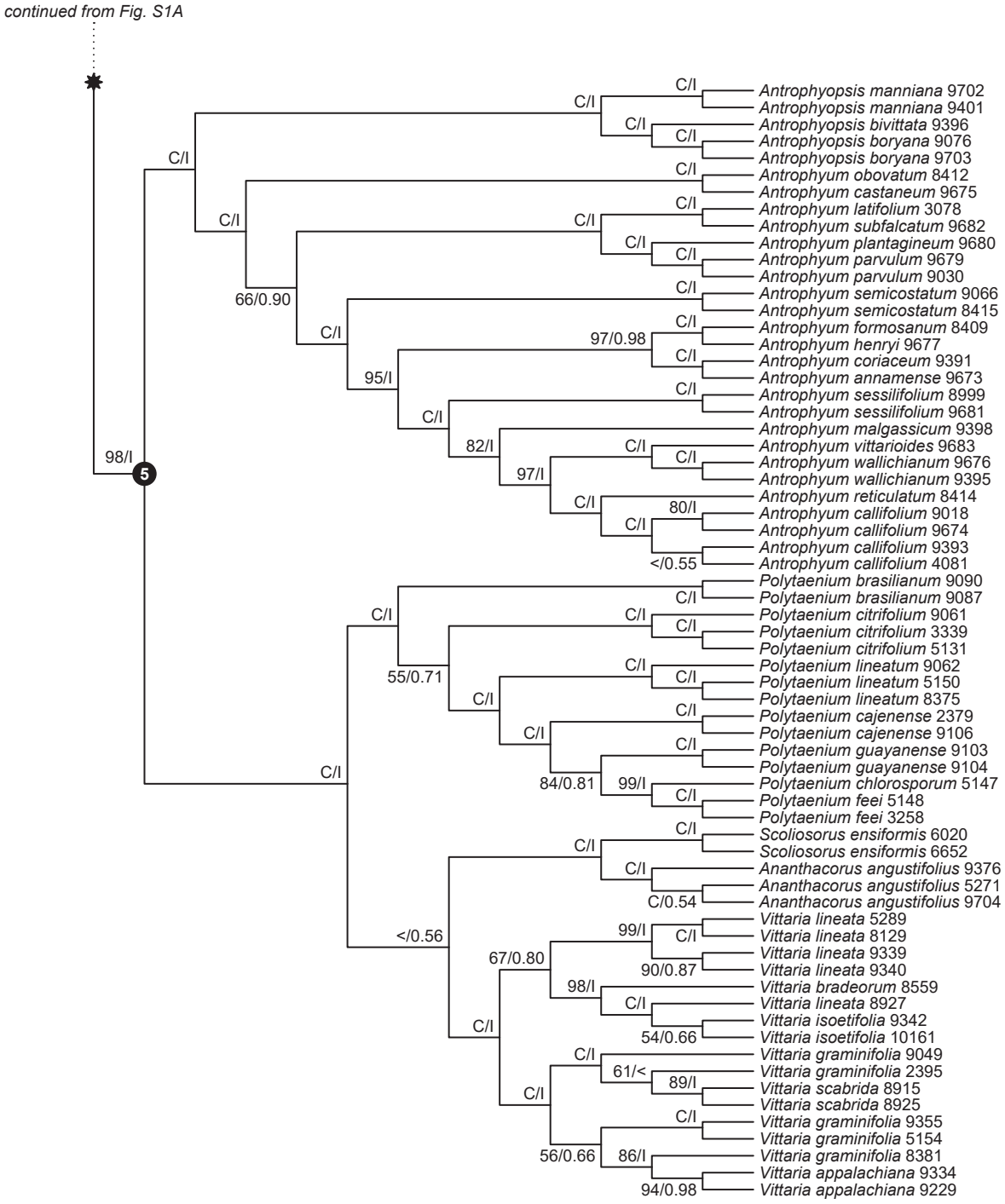

Fig. S1B. Continued from Fig. S1A.